



Out of sight, out of mind: mechanisms of social choice in fish

Ramy Ayoub, Eric Armstrong, Noam Y. Miller*

Department of Psychology, Wilfrid Laurier University, Waterloo, ON, Canada



ARTICLE INFO

Article history:

Received 22 January 2019
 Initial acceptance 25 February 2019
 Final acceptance 27 May 2019
 Available online 13 August 2019
 MS. number: A19-00053R

Keywords:

cognition
 collective behaviour
 conformity
 social learning
 zebrafish

The costs and benefits that come from being part of a group have most often been categorized by their adaptive function, such as reducing predation risk or increasing foraging competition. However, collective behaviours may also be characterized by several different behavioural mechanisms. For example, individuals may have a relatively fixed attraction to any group, as well as being able to flexibly use the information they derive from observing the group to make choices. We label these two mechanisms 'fixed' and 'informational'. In most situations, both mechanisms encourage group cohesion. Here, we placed fixed and informational mechanisms in conflict by training zebrafish, *Danio rerio*, to move away from or ignore a conspecific group in order to find food. Fish failed to learn the task when the group was visible to them while making their choice, but they were able to learn the task when the group was visually obscured. Fish trained to approach the group to find food were able to learn to do so under both conditions. Our results suggest that fish exhibit a prepotent group-joining response, even when this is potentially maladaptive – a type of conformity. This response can be inhibited under certain conditions, such as when the group is not immediately visible.

© 2019 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

A wide range of species, from humans to ants, spend much of their time in groups, and collective phenomena therefore have a large effect on individual behaviour (Krause & Ruxton, 2002). Behaviours that maintain groups benefit animals in many ways, such as by reducing predation risk or improving foraging, but may also have associated costs, such as increased competition for resources (Krause & Ruxton, 2002). These various costs and benefits to an individual resulting from being part of a group have most often been categorized by their adaptive function, the contribution they make to an animal's fitness (Krause & Ruxton, 2002). However, as noted by Tinbergen (1963), behaviour may be studied on several levels. The behaviours that maintain group cohesion may rely on a variety of (proximal) mechanisms. For example, remaining close to a group of conspecifics might result from a relatively fixed attraction towards any group, or from the individual having learned that food is more likely near large groups of conspecifics, or from a combination of both these effects (as well as others). In other words, a variety of cognitive mechanisms – by which we mean the processes that produce behaviour, such as learning or decision making (Shettleworth, 2010) – may be involved in collective behaviours. One way to expose which kinds of mechanisms affect any

given behavioural choice is to explore whether and in what ways environmental factors can change those behaviours. For example, sticklebacks' probability of copying a forging choice that they observe is flexible, depending, among other things, on how recent their own experience of the environment is (Van Bergen, Coolen, & Laland, 1994).

Some of the advantages conferred by grouping, such as predator dilution, depend mostly on individuals remaining close to a group. We might therefore expect such behaviours to be mediated by a relatively fixed attraction to the group, which does not depend on details of the situation. We label such mechanisms 'fixed'. Other benefits of grouping, however, consist of information that the group provides about the environment. The mechanisms underlying these behaviours might be sensitive to changes in how informative the group is in a particular situation, and we label these 'informational' (since they should drive behaviour in a way that depends on the information extracted from the group's actions). Such flexible mechanisms have been suggested as the basis of cognition, or 'goal-directed behaviour' (Dickinson & Balleine, 2000). Conversely, failures to adjust behaviours to environmental changes have been taken as evidence of fixed mechanisms (Hershberger, 1986). Of course, many cognitive mechanisms are partly flexible and partly fixed, and some mechanisms may be involved in several social effects. For example, if groups are usually informative about the location of food, animals might have a fixed attraction to the group for that reason.

* Correspondence: N. Y. Miller, Department of Psychology, Wilfrid Laurier University, 75 University Avenue West, Waterloo, ON, N2L 3C5, Canada.
 E-mail address: nmiller@wlu.ca (N. Y. Miller).

Under most circumstances, both fixed and informational mechanisms will act to increase or maintain group cohesion. In other words, groups are usually both innately attractive and informative, and the effects of the two mechanisms are often summed and therefore confounded (Miller, Garnier, Hartnett, & Couzin, 2013). As a result, from a purely informational perspective, individuals will appear to disproportionately copy the most common behavioural choice demonstrated by their group, a behaviour that has been labelled 'conformity' (Boyd & Richerson, 1985; Hoppitt & Laland, 2013). Conformity, by this definition, has been demonstrated in a wide range of species, from humans (Asch, 1955; Cohen, 1963; Deutsch & Gerard, 1955; Edelson, Sharot, Dolan, & Dudai, 2011) and other primates (van Leeuwen & Haun, 2013) to rats (Galef & Whiskin, 2008), birds (Aplin, Sheldon, & McElreath, 2017) and fish (Miller et al., 2013; Webster & Laland, 2012). The perspective we present above suggests that some cases of conformity may be a result of copying for other, fixed, reasons, an explanation that has been suggested to account for some human conformity (Bond & Smith, 1996).

Under some circumstances, it should be possible to place fixed and informational considerations in conflict, to separate the effects of the two kinds of mechanisms. Hershberger (1986) attempted to train domestic cockerel chicks, *Gallus gallus domesticus*, to move away from a food bowl in order to receive the food; the chicks failed to learn this unnatural response, suggesting that approaching a food source is mediated by a relatively fixed mechanism in this species. In some species, there may be advantages to maintaining some distance from a group, for example to minimize competition over food (Miller & Gerlai, 2008). If individuals primarily compete over food, the location of a group of conspecifics may be counter-informative: food is less likely to be available near the group. Members of such species will sometimes be faced with a choice between their fixed response – joining a group of conspecifics, which increases their safety – or learning to flexibly avoid the group when necessary – which may improve their foraging success. As protection from predation is likely to be a more pressing concern than any individual meal, we may expect animals to most often choose joining the group (i.e. a version of the life-dinner principle may be said to apply at the individual level; Dawkins &

Krebs, 1979). Here, we attempted to experimentally separate the two proposed mechanisms of social choice to make the effects of each one explicitly measurable.

We trained individual zebrafish, *Danio rerio*, to locate a food reward in one of two feeding rings on opposite sides of a tank (see Fig. 1, inset). Subject fish were presented with a stimulus group of five conspecifics – that they could see but not join – on one, randomly varying, side of the tank. A food reward was available either always on the side towards the stimulus group (Approach group), always on the side away from the stimulus group (Avoid group), always on the same side, independent of the stimulus group's location (Side group), or on both sides (Both group). In other words, for some fish, approaching the group led to finding food (Approach group), while others had to learn to ignore (Side group) or consistently avoid (Avoid group) their conspecifics. The Both group served as a control for the attraction of subject fish to the stimulus group in our apparatus.

As noted above, it is likely that approaching a group of conspecifics is itself rewarding to schooling fish, and learning to inhibit this prepotent response in order to obtain food may be difficult, in the same way that animals (and human infants) often fail to inhibit a reaching response for a reward that is blocked by a transparent barrier which they must detour around (Diamond, 1981; Santos, Ericson, & Hauser, 1999). In such detour experiments, subjects often perform better when the barrier to be circumvented is opaque, hiding the reward, and possibly weakening the prepotent reaching response (McLean et al., 2014). We therefore conducted a second experiment with the same four conditions as above but, on each trial, shortly before the subject fish was allowed to make its choice, we lowered an opaque barrier that prevented the subject from seeing the stimulus fish (groups Approach-Bar., Avoid-Bar., Side-Bar., Both-Bar.).

Subjects in our groups – with the exception of groups Side and Side-Bar. – had no personal information about which side of the tank was more likely to contain food. Their only cue to locating the reward was the location of the stimulus group, which varied randomly from trial to trial (i.e. the food was always located relative to the location of the group). Fish in the barrier groups were still able to see the stimulus group on each trial before the barrier was

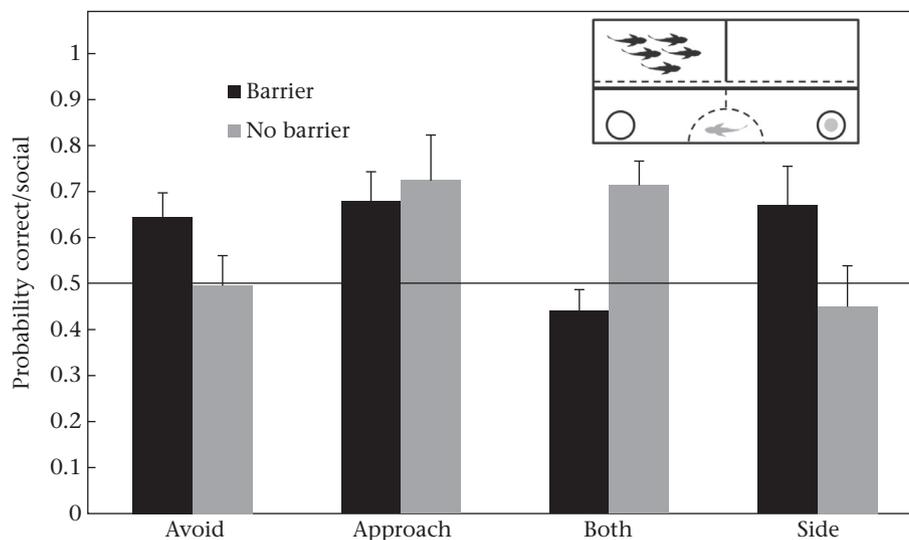


Figure 1. Proportion of test trials on which subject fish selected the correct (groups Avoid, Approach, Side) or social (group Both) side of the tank. Black bars show data from groups for which an opaque barrier separated the subject fish from the stimulus group at the time of choice; grey bars show groups where there was no barrier. The horizontal line indicates chance levels. Error bars show +SE. The inset shows a schematic of the experimental tank; dotted lines indicate transparent walls, solid lines are opaque walls. The thick solid horizontal line in the centre is a removable opaque barrier. The grey circular dot shows an example location of the reward (e.g. for the Avoid group). The subject fish is shown in grey, the stimulus group in black.

lowered and could use this information to determine where the food was. However, they could not see the group when making their choice. Subject fish in the other groups could see the stimulus fish throughout the trial.

We predicted that fish that could see the stimulus group while choosing a side of the tank would be strongly attracted to the group, causing them to approach that side whether or not it led to finding the food. However, when the group was hidden shortly before they made a choice, we predicted that subject fish would learn to choose the rewarded side of the tank, even if this meant moving away from the group they had seen, possibly because the no-longer visible group would be less attractive.

METHODS

Subjects

Subjects were 92 adult wild-type zebrafish, purchased from a local pet store (Big Al's, Kitchener, ON, Canada). A further 10 fish died before completing the experiment and their data were excluded from all analyses. A further 50 zebrafish were used as stimulus fish. Fish were housed in 10-litre tanks in an automated high-density fish rack (Pentair Aquatic Habitats) in groups of 10–15 for at least 2 weeks prior to the start of the experiment, to reduce stress. The water in the rack was maintained at $25 \pm 2^\circ\text{C}$, salinity was kept between 500 and 700 ppm TDS, and the pH was kept between 6.8 and 7.2. Except as described below, fish were fed ad libitum twice per day on commercial flake food (Big Al's Flake Food) or brine shrimp (hatched in-house).

Apparatus

Fish were tested in a tank divided into three separate compartments (see Fig. 1, inset). The tank was 40×24 inches and 10 inches high (101.6×61 cm and 25.4 cm high) and made of 1/4-inch (0.635 cm) thick white acrylic. The front section of the tank contained two floating plastic feeding rings (Nutrafin Max feeding ring, 3-inch (7.62 cm) diameter, blue with a white foam bottom) affixed to the two sides (circles in Fig. 1, inset) and a start box in the centre, which was a half-cylinder made of transparent plastic within which the subject fish could be restrained (semicircle in Fig. 1, inset). The start box could be raised and lowered manually, using fishing wire, to release the fish into the front compartment. Attached to the start box was a transparent plastic wall that extended to the wall separating the front and back compartments and which rose with the box, so that when the start box was lowered, the front compartment was divided into two sections, each containing only one feeding ring. Thus, when a subject had made a choice, it could be confined to the area of the chosen feeding ring by lowering the start box. The back part of the tank was divided into two large compartments (each 20×14 inches, 50.8×35.56 cm) by a white (opaque) wall and contained five stimulus fish on one side. The wall separating the front from the back compartments was made of transparent acrylic so that the test fish could see into the back compartments.

An additional white opaque barrier was placed in front of the transparent wall separating the front and back parts of the tank (thick black horizontal line in Fig. 1, inset). This barrier could be raised or lowered manually to block the subject's view of the stimulus fish compartments.

The tank was filled with system water taken from the housing rack, to a depth of 12.7 cm. The tank was drained and the water replaced once per week during the experiment. When the experiment was over each day, two submersible heaters, a filter and two aeration stones were placed in the tank overnight. Before the start

of the experiment each day, the water in the tank was tested for salinity and water level and was topped up or diluted as necessary to maintain it within the range of the housing rack water. The walls between the compartments of the tank were not water-tight.

The testing tank was placed on a large metal cart surrounded by white shower curtains to block any external visual cues. A video camera (Sony HDR-CX900) was attached to the top of the cart so that the entire tank was visible in the image. A monitor connected to the video camera was placed on top of the cart so that trials could be monitored.

Procedure

At least 4 days before the start of the experiment, subject fish were injected with subcutaneous visible elastomer tags (VIE, Northwest Marine Technologies, Shaw Island, WA, U.S.A.) on both sides of their dorsal fins in four colours, so that each fish could be individually identified. Subject fish were housed in groups of 10–15 throughout the experiment, in such a way that each fish had a unique tag combination for its tank so that it could be identified. Stimulus fish were not tagged and were housed in groups of 10 per tank.

Subject fish were food-deprived for 3 days, starting 1 day before the start of the experiment and covering the first 2 days of habituation. Following those 3 days, during the remainder of the experiment, immediately following experimental trials each day, subject fish were fed a small amount of floating food pellets (the same as the reward used in the experiment) in a feeding ring (identical to the one used in the experimental tank) placed in their home tank. Stimulus fish were fed ad libitum following the experiment every day (i.e. they were never food-deprived). All experimental trials were videorecorded. All experimental procedures conformed with Canada Council on Animal Care (CCAC) guidelines and were approved by our Institutional Animal Care Committee (protocol number R14007).

Habituation

The first 3 days of the experiment consisted of habituation trials. On the first 2 days, groups of 10–15 subject fish were placed together for 20 min into each of the three sections of the test tank (so each fish experienced all sections of the tank on each day). The start box was raised (open) during this time and no feeding rings were present in the tank. On the third day, each fish was placed individually into the start box. Five stimulus fish were placed into each of the back compartments and both feeding rings were baited with a single floating food pellet (~1 mm in diameter; Hikari Betta Bio-gold Pellets, fish@hikariusa.com). Food pellets were restricted within the feeding ring and could not float away. The subject fish was left in the start box for 2 min. The box was then raised and the fish was allowed to explore the front compartment of the tank either for 5 min or until it consumed both pellets.

Training

Following habituation, subject fish were given three trials daily of individual training, separated by at least 30 min, for 24 days. Starting on day 6 of this training period, one of every six trials (i.e. one trial every other day) was replaced with an unrewarded probe trial (see below). In each training trial, there were five stimulus fish in one semirandomly selected back compartment of the tank (the random sequence was controlled to ensure there were never more than two trials in a row with the stimulus fish on the same side), and one or both of the feeding rings (depending on the subject's group) were baited with a single food pellet. The other back

compartment was empty. Note that the stimulus fish could not approach the feeding ring as the back and front compartments were separated by a transparent barrier. The feeding rings were in place throughout the trial and the stimulus fish could not see the food pellet when it was in the baited feeding ring. A single subject fish was placed into the start box for 2 min. For some groups, the opaque barrier was lowered after 110 s. After 2 min, the start box was raised and the subject fish was allowed to make a single choice to one of the two feeding rings. A choice was registered when the fish approached to within 3 cm (approximately one body length) of one feeding ring. Once the fish had made a choice, the start box was lowered so that the fish was restricted to the side of the front compartment of the tank that it had chosen. If the fish chose the baited side, it was given up to 3 min to consume the food there and then removed. If the fish chose the unrewarded side, it was left there for 2 min and then removed. If the fish made no choice within 3 min, it was removed from the tank and the trial was excluded from analysis.

Fish were divided into eight groups. Each fish was assigned to one group for the duration of the experiment (i.e. the comparison is between subjects). For fish in group Avoid ($N = 13$), the baited food ring was always on the opposite side of the tank to the one containing the stimulus fish (so, for example, the stimulus fish could be on the right and the reward on the left for one trial and then these positions would be reversed for the next trial); for fish in group Approach ($N = 9$), the food was always on the same side as the stimulus fish; for fish in group Side ($N = 12$), the food was always on the same side (counterbalanced across subjects), irrespective of the location of the stimulus fish (which still changed sides semirandomly from trial to trial); for fish in group Both ($N = 11$), both feeding rings contained food on every trial (and the stimulus fish still changed sides semirandomly). The remaining four groups were identical to these four, except that the opaque barrier was lowered 20 s before the subject fish was released, blocking their view of the stimulus fish at the time of choice. These groups were labelled Avoid-Bar. ($N = 15$), Approach-Bar. ($N = 13$), Side-Bar. ($N = 11$) and Both-Bar. ($N = 9$).

Probe Tests

Beginning on day 6 of training, one semirandomly selected trial every other day was replaced with a probe test trial (i.e. one trial out of every 6). The probe trial was never the first trial of the day. Probe trials were identical to training trials, except that there was no food in either feeding ring. Using unrewarded trials is a standard procedure in testing for learning experiments (e.g. Shettleworth, 2010, p. 255). In this case, having no food in the tank during probe trials ensured that fish could not use odour cues to find the food. Fish were removed from the tank as soon as they had made a choice to one of the two feeding rings. We exclude the data from probe trials run before day 12 of training, as most fish had not yet learned the task (see Appendix, Fig. A1). Thus, we report the results of seven probe trials per subject (on days 12, 14, 16, 18, 20, 22, 24). Each fish was given a score based on the proportion of these seven probe tests on which it chose the rewarded side of the tank (or, for groups Both and Both-Bar., the side containing the stimulus group).

Analysis

Choice data for all training trials and probe tests were entered into a Microsoft Excel spreadsheet. Statistical tests were conducted using the BayesFactor and BEST (Kruschke, 2012) packages in R (R Core Team, 2013). For probe test data, each subject was given a score based on the proportion of its seven probe tests on which it chose correctly (i.e. chose the side with the food). For groups Both

and Both-Bar., for which both sides were rewarded, we calculated the proportion of tests on which they chose the side containing the stimulus group, which we call the social choice. We conducted a Bayesian estimation of each group's mean performance (μ), standard deviation (σ) and effect size (Appendix, Table A1). Means were compared to chance levels by testing whether 95% or more of the posterior distribution of the mean was above 0.5, which is comparable to performing a one-sample t test (Kruschke, 2012). We also calculated the Bayes factor (BF) across all groups for both the probe data (one-way Bayesian ANOVA by group, with identity (ID) as a random factor) and the training data (mixed-effect Bayesian ANOVA by group and training trial block, with ID as a random factor). In the main text, we report the mean of the posterior distribution on the group mean (mean- μ) and the Bayes factor (BF) for all parameter estimates, along with effect size labels as suggested by Jeffreys (1961). Briefly, the Bayes factor is the ratio of the likelihoods of the two hypotheses (for example, that the group's performance on probe trials was better than chance versus not better than chance): factors larger than one suggest that the tested hypothesis is more likely than the alternative (null) hypothesis. So, a factor of five means that the tested hypothesis is five times more likely than the alternative. We report Bayes factors for comparisons of each group's performance to chance, as well as comparisons between groups with and without a barrier (comparable to performing a two-sample t test; Kruschke, 2012). All other measures are given in Table A1 and in the captions to Fig. 2 and Fig. A1. The data are available on our Open Science Framework repository: <https://osf.io/h97uf/>.

RESULTS

When the stimulus group was visible to the subject throughout the trial, we found anecdotal evidence (Jeffreys, 1961) that zebrafish were able to learn to approach a group of conspecifics (Approach group: mean- $\mu = 0.73$, BF = 1.86; Fig. 1, grey bars; Table A1) and, when food was available on both sides of the tank, strong evidence that they preferred the side closest to the group (Both group: mean- $\mu = 0.71$; BF = 24.58). However, we found moderate evidence that the fish failed to learn to avoid (Avoid group: mean- $\mu = 0.50$; BF = 0.28) or ignore (Side group: mean- $\mu = 0.46$; BF = 0.33) a visible group of conspecifics to locate a food reward.

When the stimulus fish were hidden at the time of choice, we found moderate evidence that zebrafish were able to learn to move away from (Avoid-Bar. group: mean- $\mu = 0.65$; BF = 5.09; Fig. 1, black bars) or ignore (Side-Bar. group: mean- $\mu = 0.68$; BF = 1.35) a group of hidden conspecifics in order to locate food. We also found moderate evidence that fish were able to learn to approach the group (Approach-Bar. group: mean- $\mu = 0.68$; BF = 4.54). When food was available on both sides of the tank, we found anecdotal evidence that they showed no preference for either side (Both-Bar. group: mean- $\mu = 0.44$; BF = 0.61), suggesting that hiding the group at the time of choice primarily served to make that side of the tank less immediately appealing.

We next compared groups tested without a barrier to those tested with the barrier. We found either anecdotal or no evidence for an effect of the barrier in the Avoid (Avoid versus Avoid-Bar., BF = 1.28), Approach (Approach versus Approach-Bar., BF = 0.41) or Side (Side versus Side-Bar., BF = 1.18) groups, and we found strong evidence of a decrease in attraction to the social side in the Both group when the barrier was added (Both versus Both-Bar., BF = 28.68). To examine whether fish that had to avoid or ignore the group had any motivation to do so, even if it was partially masked by their attraction to the group, we compared their choices to those of the Both group, which could find food on either side of the tank and whose choices should therefore simply reflect their

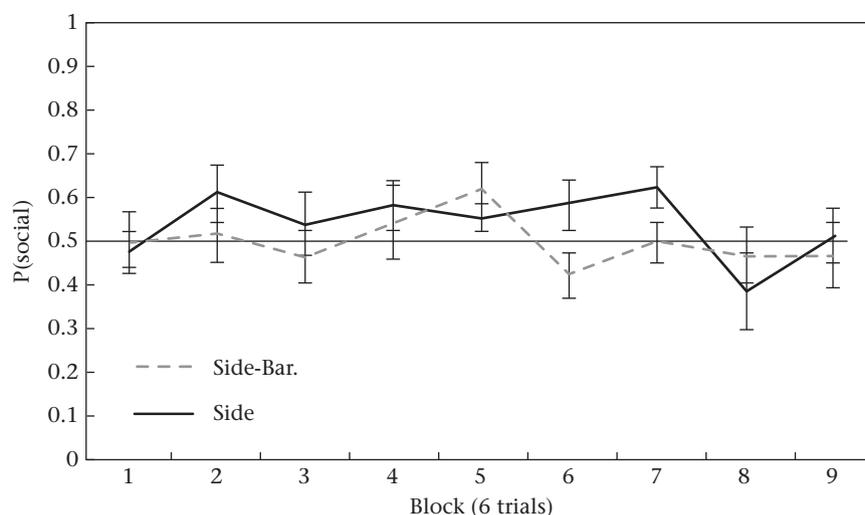


Figure 2. Proportion of training trials (in blocks of 6 trials each) on which the groups for which the food was always on the same side (Side = black; Side-Bar. = grey) chose the side that contained the stimulus group, whether or not that side was rewarded. Error bars show \pm SE.

attraction to the group. We found a moderate difference between the groups (Avoid versus Both, $BF = 3.76$; Side versus Both, $BF = 3.36$), suggesting that subjects in the Avoid and Side group were not simply following the stimulus group.

For groups Side and Side-Bar., the location of the stimulus group was irrelevant to the task, as the food reward was always on the same side of the tank. It is still possible, however, that these subjects' choices were driven by the position of the conspecific group. We therefore tested whether their choices were more often to the side containing the stimulus group, whether or not that side was rewarded (Fig. 2). We found no evidence for a main effect of group or block, nor any interaction (group-only model, $BF = 0.33$; block only, $BF = 0.14$; group + block, $BF = 0.05$; group + block + group:block, $BF = 0.005$), strongly suggesting that these fish did not simply adopt a strategy of approaching (or avoiding) the stimulus group.

DISCUSSION

When a group of conspecifics was visible on one side of a tank, zebrafish that could find food on either side of the tank (Both group) preferred to move towards the group. However, fish that were required to move away from their conspecifics in order to find food (Avoid group) failed to learn to do so. On test trials, these fish did not consistently approach the group, but simply performed at chance (approaching the group less often than fish in the Both group), possibly reflecting contradicting behavioural motivations. Similarly, fish for whom the location of the stimulus group was irrelevant to finding food (Side group) also failed to learn to locate the food (and also did not simply approach their conspecifics on test trials). Fish that could only find the food by moving towards the group (Approach group) were able to learn the task. These results suggest that when placed in our testing tank – a featureless white and brightly lit environment – the sight of a group of conspecifics is sufficiently attractive to a solitary subject that it generally overrides any other motivation.

It is likely that the failure of these fish to learn to move towards the food reflects the attractiveness of a group of conspecifics. Zebrafish spend almost all their time in groups and a solitary fish, like our subjects, will quickly move to rejoin a group. Indeed, the presence of a group of conspecifics is frequently used as a reward to motivate learning (Al-Imari & Gerlai, 2008). In an attempt to make it easier to inhibit this prepotent response, possibly unmasking

another mechanism that is flexibly responsive to the location of food, we lowered an opaque barrier between the subject fish and the stimulus group. We allowed subjects to see the group first on every trial, but blocked their sight of the group shortly before they were released to make their choice. Under these conditions, we found that the group was no longer as attractive. Fish that could find food on either side of the tank (Both-Bar. group) no longer showed a preference for the side containing the stimulus group, and fish for whom the group's location was uninformative (Side-Bar. group) were able to learn to ignore the group to find food.

These results do not, however, indicate that fish forgot where the group was when we lowered the visual barrier. As the stimulus group was moved randomly from trial to trial, fish that could only find food by approaching (Approach-Bar. group) or moving away from (Avoid-Bar. group) the group still had to use the location of the group, which they observed at the start of each trial before the barrier was put in place, to drive their choices. Both groups were able to learn to do so, and consistently found the food.

Our data show that individual zebrafish can be trained to avoid or ignore a group of conspecifics in order to find food, but only if their prepotent response of joining (or at least approaching) the group is inhibited by visually obscuring the group at the time of choice. It is likely that hiding the group reduces subject fish's motivation to join the group, revealing their learned ability to locate the food. When the group remains visible at the time of choice, fish do not move away from it to find food, possibly reflecting either that they have not learned the response or that the attraction of the group overwhelms it.

There are other possible mechanisms that may have affected our results. We did not monitor the behaviour of the stimulus group during the trials, and it is possible that the movements of these fish somehow cued the subject fish and affected their choices. However, we ensured that the stimulus fish could not see where the food was located (and on probe trials there was no food to detect) and it is not clear how they might have cued the subject fish. Similarly, it is not clear why the same stimulus fish would behave differently across our different groups.

Our results suggest that at least two distinct mechanisms drive social choice in zebrafish, which we label 'fixed' and 'informational'. By manipulating the accuracy of a conspecific group in predicting the location of a food reward, we are able to tease apart the contributions of each mechanism. We show that fixed mechanisms of attraction to

a group prevail when the group is visible at the time of choice, causing subjects to approach the group even when that never leads to reward – a form of conformity – but that informational mechanisms can overcome the tendency to conform when the group is hidden during choice. It is possible that this apparent predominance of fixed over informational considerations results from the difference in potential consequences of each choice (Dawkins & Krebs, 1979).

Studies of social influence in humans have sought to distinguish between fixed and informational mechanisms of conformity, often labelled compliance and internalization (Kelman, 1958), normative and informational (Deutsch & Gerard, 1955) or private and public (Edelson et al., 2011), usually – as here – by presenting subjects with collective opinions that are obviously wrong (Asch, 1955). In such cases, informational considerations should drive subjects to ignore or contradict the group's choice, whereas fixed (normative) considerations will still promote copying the group's decision, much as in our Avoid group. In human studies, where between one-third and two-thirds of subjects will conform to an obviously incorrect group of peers (Asch, 1955; Cohen, 1963; Deutsch & Gerard, 1955; Edelson et al., 2011), conformity has sometimes been shown to decrease when subjects give their responses anonymously (Asch, 1955; Sunstein, 2003; but see ; Bond & Smith, 1996; Deutsch & Gerard, 1955). Such results have been cited as evidence that human subjects generally conform – despite being aware that their responses are incorrect – due to normative pressures, which are reduced when the group does not have access to a subject's responses (Sunstein, 2003). This effect is similar, at least on the surface, to our addition of an opaque barrier between the subject fish and the stimulus group, which also reduced conformity in the fish.

There is an extensive literature on decision making in social contexts in fish, most of which aligns well with our results. Nine-spine sticklebacks, *Pungitius pungitius*, will copy the foraging choice of a group of conspecifics more when their own information about feeding locations is less reliable or was gathered less recently (Van Bergen et al., 1994), and they will preferentially copy the larger of two groups or the group feeding from a richer feeder (that dispenses food more frequently; Pike & Laland, 2010; we note, incidentally, that our experimental tank was inspired by the one used in these papers). These results delimit some of the flexibility in the mechanism driving social choice in this species. Sticklebacks are not equally attracted to any group of conspecifics but take into account their own information about the distribution of resources and the behaviours they observe their conspecifics performing (i.e. are they feeding frequently or not). Sticklebacks will choose the side of the tank that previously held a smaller group of fish (of 2) feeding from a richer feeder over the side that held a larger group (of 6) feeding from a poor feeder (Coolen, Ward, Hart, & Laland, 2005).

Many collective effects undoubtedly rely on a combination of the two types of mechanisms we discuss. For example, predator confusion (Miller, 1922) may be enhanced by both physical similarities between members of a group (i.e. the absence of an oddity effect; Landeau & Terborgh, 1986) as well as by the coordination of a group's movement (the lack of 'behavioural oddity'; Bode, Faria, Franks, Krause, & Wood, 2010). In addition, it is likely that other behavioural mechanisms beyond the two we identify play a role in coordinating and shaping collective behaviours. Future research on the modulators of these mechanisms may help to uncover how animals balance conflicting imperatives when making decisions in a socially complex world.

Author Contributions

R.A. and N.Y.M. conceived the study; R.A. and E.A. ran the experiments and coded the videos; all authors analysed the data and drafted the manuscript.

Declarations of Interest

None.

Acknowledgments

We thank Mackenzie Schultz and other members of the Collective Cognition Lab for assistance in running the experiments, and Kelley Putzu for assistance with animal care. The research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant (RGPIN-2016-06138) and a Banting Research Foundation Award (2016-1387) to N.Y.M.

References

- Al-Imari, L., & Gerlai, R. (2008). Sight of conspecifics as reward in associative learning in zebrafish (*Danio rerio*). *Behavioural Brain Research*, *189*, 216–219.
- Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 7830–7837.
- Asch, S. E. (1955). Opinions and social pressure. *Scientific American*, *193*, 31–35.
- Bode, N. W. F., Faria, J. J., Franks, D. W., Krause, J., & Wood, A. J. (2010). How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society B*, *277*, 3065–3070.
- Bond, R., & Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) line judgment task. *Psychonomic Bulletin*, *119*, 111–137.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Cohen, A. P. (1963). *Conflict and conformity: A probability model and its application*. Boston, MA: MIT Press.
- Coolen, L., Ward, A. J. W., Hart, P. J. B., & Laland, K. N. (2005). Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behavioral Ecology*, *16*, 865–870.
- Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society B*, *205*, 489–511.
- Deutsch, M., & Gerard, H. B. (1955). A study of normative and informational social influences upon individual judgment. *Journal of Abnormal and Social Psychology*, *51*, 629–636.
- Diamond, A. (1981). Retrieval of an object from an open box: The development of visual–tactile control of reaching in the first year of life. *Society for Research in Child Development Abstracts*, *3*, 78.
- Dickinson, A., & Balleine, B. W. (2000). Causal cognition and goal-directed action. In C. Heyes, & L. Huber (Eds.), *Vienna series in theoretical biology. The evolution of cognition* (pp. 185–204). Cambridge, MA: MIT Press.
- Edelson, M., Sharot, T., Dolan, R. J., & Dudai, Y. (2011). Following the crowd: Brain substrates of long-term memory conformity. *Science*, *333*, 108–111.
- Galef, B. G., & Whiskin, E. E. (2008). Conformity in Norway rats? *Animal Behaviour*, *75*, 2035–2039.
- Hershberger, W. A. (1986). An approach through the looking glass. *Animal Learning & Behavior*, *14*, 443–451.
- Hoppitt, W., & Laland, K. N. (2013). *Social learning*. Princeton, NJ: Princeton University Press.
- Jeffreys, H. (1961). *Theory of probability*. Oxford, U.K.: Oxford University Press.
- Kelman, H. C. (1958). Compliance, identification, and internalization: Three processes of attitude change. *Conflict Resolution*, *2*, 51–60.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
- Kruschke, J. K. (2012). Bayesian estimation supersedes the *t* test. *Journal of Experimental Psychology: General*, *142*, 573–603.
- Landeau, L., & Terborgh, J. (1986). Oddity and the 'confusion effect' in predation. *Animal Behaviour*, *34*, 1372–1380.
- van Leeuwen, E. J. C., & Haun, D. B. M. (2013). Conformity in nonhuman primates: Fad or fact? *Evolution and Human Behavior*, *34*, 1–7.
- McLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, E2140–E2148.
- Miller, R. C. (1922). The significance of the gregarious habit. *Ecology*, *3*, 122–126.
- Miller, N. Y., Garnier, S., Hartnett, A. T., & Couzin, I. D. (2013). Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 5263–5268.
- Miller, N. Y., & Gerlai, R. (2008). Oscillations in shoal cohesion in zebrafish (*Danio rerio*). *Behavioural Brain Research*, *193*, 148–151.
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, *6*, 466–468.
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Santos, L. R., Ericson, B. N., & Hauser, M. D. (1999). Constraints on problem solving and inhibition: Object retrieval in cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *113*, 186–193.

- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). Oxford, U.K.: Oxford University Press.
- Sunstein, C. R. (2003). *Why societies need dissent*. Boston, MA: Harvard University Press.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.
- Van Bergen, Y., Coolen, I., & Laland, K. N. (1994). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B*, 271, 957–962.
- Webster, M. M., & Laland, K. N. (2012). Social information, conformity and the opportunity costs paid by foraging fish. *Behavioral Ecology and Sociobiology*, 66, 797–809.

Appendix

Table A1

Bayesian parameter estimation for probe trial data

Group	Mean- μ	HDI	BF	Mean- σ	Mean-ES	P (ROPE)
Avoid	0.499	(0.351, 0.643)	0.278	0.216	0.032	0.26
Approach	0.731	(0.489, 0.986)	1.862	0.292	0.725	0.04
Side	0.456	(0.265, 0.661)	0.328	0.288	0.166	0.24
Both	0.709	(0.588, 0.831)	24.577	0.164	1.180	0
Avoid-Bar.	0.650	(0.534, 0.763)	5.088	0.200	0.690	0.01
Approach-Bar.	0.682	(0.533, 0.821)	4.538	0.217	0.715	0.02
Side-Bar.	0.679	(0.467, 0.878)	1.347	0.275	0.652	0.05
Both-Bar.	0.442	(0.324, 0.554)	0.606	0.131	0.323	0.13

Shown are results of Bayesian estimation of each group's probe trial data (see Methods). Mean- μ : the mean of the posterior distribution on the group mean proportion correct (or social, for the Both and Both-Bar. groups); HDI: 95% highest density interval of the posterior distribution on the group mean; BF: Bayes factor; Mean- σ : mean of the posterior distribution on the standard deviation; Mean-ES: mean of the posterior distribution on the effect size; P (ROPE): proportion of the effect size posterior distribution that fell within the interval $[-0.1, 0.1]$, sometimes called a region of practical equivalence (ROPE). Rows for which the analysis supports the hypothesis that the group mean is larger than 0.5 ($BF > 1$) are shown in bold.

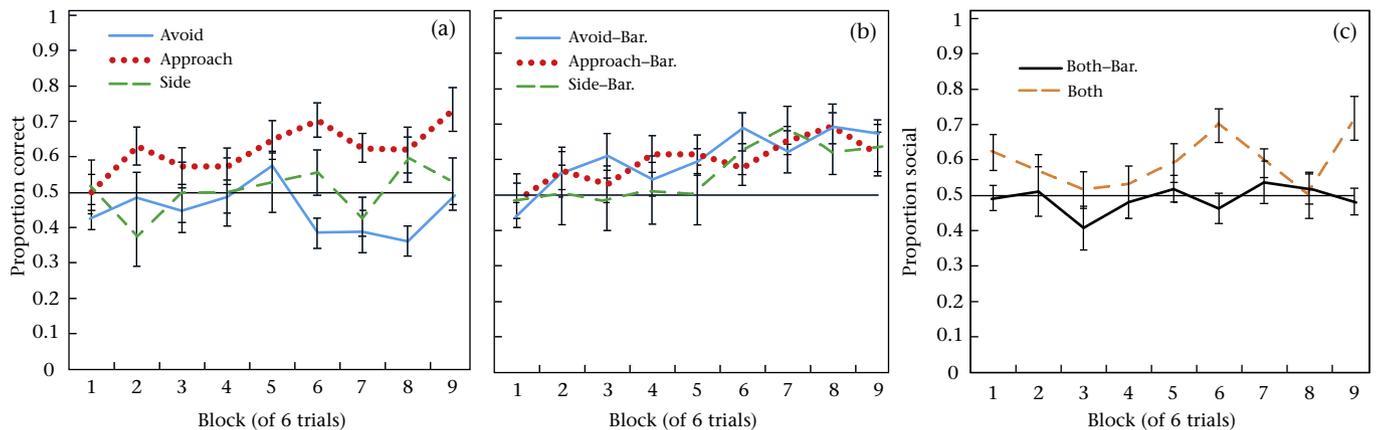


Figure A1. Proportion of correct (or social) choices by group for successive blocks of six training trials each: (a) groups Avoid (solid blue), Approach (dotted red) and Side (dashed green); (b) groups Avoid-Bar. (solid blue), Approach-Bar. (dotted red) and Side-Bar. (dashed green); (c) groups Both (dashed orange) and Both-Bar. (solid black). The black horizontal line in each panel shows chance levels. Error bars show \pm SE. The most likely model strongly suggested main effects of both group and training block but no interaction (Bayes factors: group only = 38.79; block only = 1.84; group + block = 61.82; group + block + group:block = 2.96).